

EFFECTS OF SIMULATED ELK GRAZING AND TRAMPLING (I): INTENSITY

Susan P. Rupp^{1,3}, Mark C. Wallace¹, David Wester¹, Stephen Fettig², and Robert Mitchell¹

¹ Department of Range, Wildlife, and Fisheries Management, Box 42125, Texas Tech University, Lubbock, TX 79409-2125, USA; ² Bandelier National Monument, HCR 1 Box 15, Los Alamos, NM 87544-9701, USA

ABSTRACT: Vegetative impacts caused by Rocky Mountain elk (*Cervus elaphus nelsoni*) grazing and trampling have been a growing concern for natural resource managers. The threat to archeological resources and naturally functioning ecosystems as a result of excessive elk trampling and grazing now rank as the highest management priority at Bandelier National Monument (BAND), New Mexico. In summer 1998, BAND erected a series of ungulate exclosures and paired reference areas to evaluate elk impacts on the vegetative community in piñon-juniper (*Pinus edulis* – *Juniperus* spp. [PJ]), ponderosa (*Pinus ponderosa*) grassland, and mixed-conifer (MC) habitat types. We evaluated simulated grazing/trampling treatment combinations applied at different intensities from January through May of 1999 and 2000. Litter cover was negatively correlated with clipping intensity in PJ and MC sites. Trampling more consistently impacted parameters and may stimulate plant productivity at an intermediate intensity, especially in terms of forb response. Longer time periods may be needed to detect vegetative responses to changes in grazing pressure especially in ecosystems that have developed with a history of grazing pressure.

ALCES VOL. 37 (1): 129-146 (2001)

Key words: *Cervus elaphus nelsoni*, elk, grazing, New Mexico, trampling

Grazing systems are partially defined by the intensity (amount of plant material removed) and frequency (the number of times a plant is defoliated) of use which, in turn, affects both the quality and quantity of forage produced (Motazedian and Sharrow 1990). Few studies have attempted to isolate the effects of intensity or frequency of use (Gillen et al. 1990) and it is often unclear whether effects are caused by the removal of vegetation or associated trampling. Studies have isolated effects of grazing (Oesterheld 1992) or trampling intensity (Warren et al. 1986, Abdel-Magid et al. 1987, Tollner et al. 1990), but have ignored possible interactive effects. In addition, kind of animal, season and intensity of use,

soil characteristics, individual plant and community characteristics (e.g., density, morphology, physiology), and temporal and spatial variation in environmental conditions influence the type and degree of impact (Weigel et al. 1990, Bastrenta et al. 1995).

Divergent management objectives of the state of New Mexico, Los Alamos National Laboratory (LANL), Bandelier National Monument (BAND), tribal communities, and private lands hamper effective elk management (Allen 1996). Hunting on BAND is prohibited by Code of Federal Regulations (CFR), Title 36, Part 2, Sections 2.1-2.4 (Fettig 1997); any direct reduction of the elk herd would require a legislative act of Congress. Before any

³ Present address: Los Alamos National Laboratory, ESH-20 (Ecology Group), MS M887, Los Alamos, NM 87545, USA

actions can be taken, however, there is a need for quantitative, scientific information on the potential impacts of the Bandelier elk herd. Population dynamics must be evaluated and impacts to vegetative and soil communities, if any, must be quantified. The objectives of this study were to assess changes in density, percent foliar/litter cover, basal area, species richness, and composition through the application of different intensities of simulated clipping and trampling within elk exclosures.

STUDY AREA

Bandelier National Monument is located in the Jemez Mountains of north central New Mexico (35:53:38N 106:17:02W) approximately 8 km south of Los Alamos in the Pajarito Plateau (Fig. 1). It is bordered by Santa Fe National Forest to the west, LANL to the east, and private lands to the north and south. Native American reservation lands are also found throughout the surrounding areas. The monument's 13,290 ha range in elevation from 1,680 m in the lower canyons near the Rio Grande to about 3,240 m near the summit of Cerro Grande.

Vegetative patterns are dependent on elevation and topography (Wilcox and Breshears 1994). Lower elevations (1,680 - 2,015 m) are characterized as piñon-juniper (PJ) woodland and are composed of stands of piñon pine (*Pinus edulis*) and one-seed juniper (*Juniperus monosperma*) with understory shrubs of wavy leaf oak (*Quercus undulata*), Apache plume (*Fallugia paradoxa*), and mountain mahogany (*Cercocarpus montanus*) (Brown 1982). Mid-elevation transitional ponderosa (*Pinus ponderosa*) grassland (PG) areas (2,015 - 2,440 m) include an overstory of ponderosa pine and understory of Gambel oak (*Quercus gambelii*), New Mexican locust (*Robinia neomexicana*), and mountain mahogany. Typical grasses in PG include mutton grass (*Poa fendleriana*), Junegrass (*Koeleria cristata*), and mountain muhly (*Muhlenbergia montana*). Upper elevation mixed-conifer (MC) areas (2,440 - 3,240 m) have a variety of overstory species that include Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), blue spruce (*Picea pungens*), and quaking as-

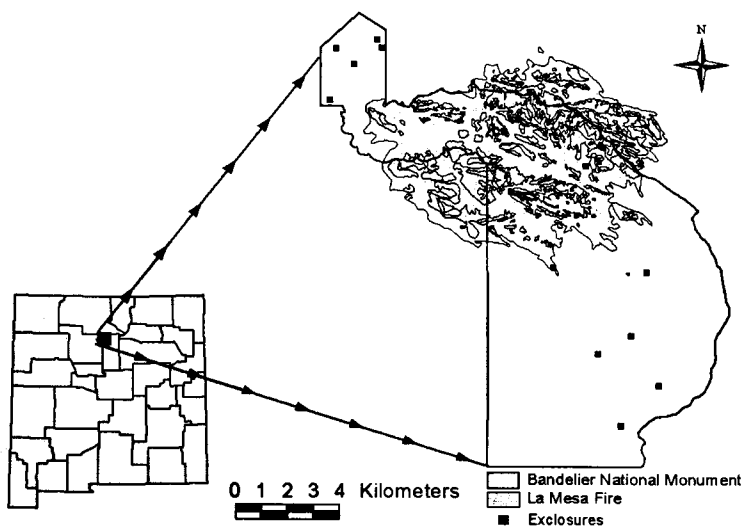


Fig. 1. Study area on Bandelier National Monument, New Mexico, 1998-2000, showing extent of the 1977 La Mesa fire and locations of the 15 elk exclosures erected in 1997.

pen (*Populus tremuloides*). Gambel oak, rock spirea (*Holodiscus dumosus*), and waxflower (*Jamesia americana*) are typical understory shrubs and slender wheatgrass (*Agropyron trachycaulum*), Canada bluegrass (*Poa compressa*), and Parry oatgrass (*Danthonia parryi*) are common grasses in the MC zone. Canyon bottoms have riparian communities that include narrowleaf cottonwood (*Populus angustifolia*) and boxelder (*Acer negundo*).

In 1977, approximately 6,180 ha of land in Santa Fe National Forest, BAND, and LANL burned in the "La Mesa" fire (Fig. 1). Sixty-nine percent, or 4,250 ha, of the total area burned was on BAND (Foxx 1984). The 1977 La Mesa fire changed available forage conditions and is believed to have contributed to a population increase of the elk herd (Allen 1996).

Average annual precipitation on the Pajarito Plateau is 330 to 460 mm (National Oceanographic and Atmospheric Administration, Climatological data, Los Alamos, NM, <http://www.ncdc.noaa.gov>, 2001) of which about 45% occurs in July, August, and September. Average daytime temperatures range from 32.2°C in the summer (max. = 41.1°C) to -9.4°C in the winter (min. = -30.6°C). Over this study, 1998 - 2000, temperatures were generally higher than the 1920 - 1999 average, except for an unseasonal cold front in April 1999. Annual precipitation during the 1998 - 1999 and 1999 - 2000 field seasons was also lower than average.

METHODS

Experimental Design

During summer of 1998, 15 60 m x 60 m ungulate exclosures (5 exclosures in each of 3 different habitats - MC, PG, and PJ) were erected on BAND. In October of 1998, a plot consisting of 12 1 m² experimental units was established inside each

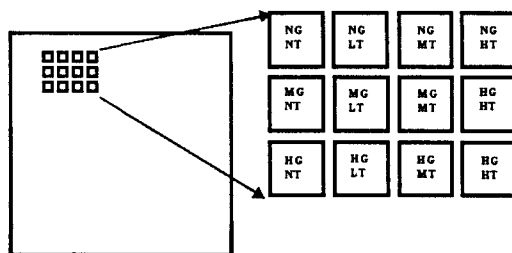


Fig. 2. Designation of clipping X trampling treatment combinations inside exclosures. Clipping treatments were applied at 100% standing crop removal either 0 (none), 1 (light), 2 (moderate), or 3 (heavy) times while trampling was applied at 0, 5, 25, or 100 footfalls/m² at 0 (none), 1 (light), 2 (moderate), or 3 times (heavy), respectively. Clipping treatments are designated with 'G' while trampling is designated with 'T'. Treatments were randomly assigned to 1-m² experimental units.

exclosure. While, because of vegetative complexity and diversity, experimental units in MC sites were 0.25 m².

A two-factor factorial, randomized block design (Steel and Torrie 1980) was used to evaluate the impacts of clipping, trampling, and their interaction. Treatments were applied at 3 clipping intensities (none [0%] moderate [40-60%], or heavy [100%] standing crop removal) and 4 trampling intensities (none [0 footfalls/m²], light [5 footfalls/m²], moderate [25 footfalls/m²], or heavy [100 footfalls/m²]) during a single treatment application (Fig. 2). A split-plot arrangement with time as a subplot factor allowed for analysis over the 2 years of the study. Treatments (clipping and/or trampling) were randomly assigned to experimental units (1 m²/0.25 m² plots) within each block (exclosure).

Clipping was used to simulate grazing while trampling was simulated using an artificial hoof cast from dental acrylic (Pro Orthodontic Services, Racine, Wisconsin, USA) molded from the front hoof print of an elk (Acorn Naturalists®, Tustin, California, USA). Two of these artificial hooves were

securely bolted to the bottom of a pair of sandals which could then be strapped on the feet of the investigator. The average front hoof load of an elk is approximately 685 g/cm² (Telfer and Kelsall 1984). For purposes of this study, applied hoof load was calculated to be in the range of 673 - 818 g/cm². This design attempted to emulate the rocking or churning effect caused by a hoof when the animal is walking, which has been overlooked in other simulated studies where mechanical devices have been used (Warren et al. 1986). Trampling in the MC plots was applied to a full 1 m² area even though effects were measured only on 0.25 m².

Pre-treatment data were collected and treatments were applied in January through May 1999 when elk normally would use each habitat type. Post-treatment data were collected and treatments were applied again during the same time periods in 2000. Variables measured included density, foliar/litter cover, basal area, productivity, species richness, and composition. Plants were identified to the species level allowing for further analysis by sub-class (i.e., grasses and forbs). Unknown plants were collected in the field and numbered for later identification.

Statistical Analysis

Analysis of variance (ANOVA) and mean separation were used to determine treatment effects within and across habitats for total density and foliar cover. Habitat effects were tested using the Type III mean square for block (habitat) as an error term. Potential block (exclosure) X treatment interactions were tested using Tukey's test for non-additivity. When sub-divided by grass and forb growth classes, density data and foliar percentages that were not normally distributed were transformed using square root or arcsine transformations, respectively (Sokal and Rohlf 1995). Experimental units which lacked a grass or forb

class were treated as sampled units and zeroes were added to the dataset. Basal area, species richness, and litter cover were only analyzed within habitats. For all analyses, significance was delineated at $\alpha = 0.10$.

RESULTS

We report results of combinations of intensity of clipping and trampling treatments. Rupp et al. (2001) examined the effects of frequency of treatments. Analyses of pre-treatment plot data revealed block (i.e., exclosure) X treatment interactions ($F_{1,43} = 31.61, P < 0.001$) for density in the PJ habitat type as well as for foliar cover in MC ($F_{1,43} = 4.09, P = 0.049$) and PJ ($F_{1,43} = 22.46, P < 0.001$) habitats. Initial block X treatment interactions were also detected in PG habitat, but removal of exclosure PG-5 that had been burned in 1998 and exclosure PG-1 that had been burned in 1999 remedied this effect for both density ($P = 0.334$) and foliar cover ($P = 0.226$) estimates. Because differences among habitats existed before treatments were applied, pre-treatment densities or foliar cover estimates were used as covariates in analysis of covariance (ANCOVA) for subsequent analyses. Litter and basal area were analyzed using ANOVA. All pre-treatment data for total density, foliar cover, and species richness were normally distributed except for foliar data in the MC zone. Litter data were normally distributed in MC and PG habitats, but failed to meet normality in the PJ zone. Attempts to normalize these data via transformation were unsuccessful and litter results for the PJ habitat type should be interpreted with caution.

Habitat Effects

A habitat effect ($F_{2,10} = 15.39, P = 0.001$) was detected for density data with more plants/m² in MC than in either PG or PJ habitats. There was a habitat by trampling interaction for foliar cover ($F_{6,110} =$

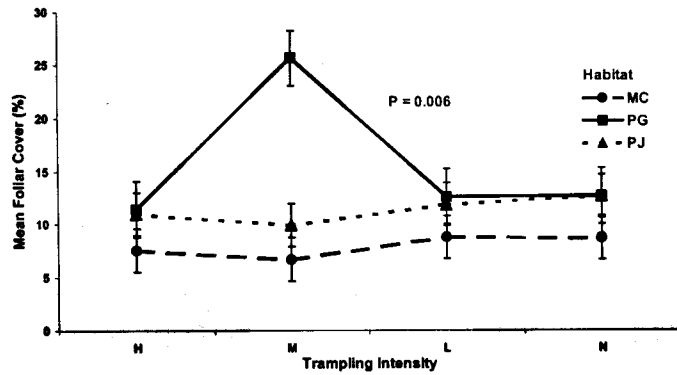


Fig. 3. Adjusted mean foliar cover (%) by habitat in response to trampling intensity (Spring 2000). The trampling X habitat interaction was significant ($F_{6,110} = 3.23, P = 0.006$). Trampling was applied at 100 (heavy), 25 (moderate), 5 (light), or 0 (none) footfalls per unit area.

3.23, $P = 0.006$) indicating that trampling treatments were not having the same effect in each habitat (Fig. 3). Moderately trampled experimental units in PG sites had significantly higher foliar cover ($\bar{X} = 25.7\%$) regardless of clipping intensity. In contrast, moderately trampled plots in the MC habitat had less foliar cover ($\bar{X} = 6.7\%$) than any other trampling treatment regardless of clipping intensity. No other significant differences were detected in density or foliar cover for clipping, trampling, or their interaction across all habitat types.

Piñon-Juniper Habitat

We detected a clipping effect ($F_{2,43} = 3.55, P = 0.038$) regardless of trampling

intensity for density measures. Mean separation of adjusted means indicated that heavily clipped plots had higher plant densities than moderately clipped or unclipped plots (Table 1). There was a trampling effect ($F_{3,43} = 2.33, P = 0.088$) on foliar cover. Moderately ($\bar{X} = 10.1\%$) trampled plots had less foliar cover than lightly trampled units ($\bar{X} = 12.9\%, P = 0.031$), but heavily ($\bar{X} = 10.4\%$) and non-trampled ($\bar{X} = 12.1\%$) areas were not different from either one.

Analysis by vegetative type revealed an effect ($F_{3,43} = 2.50, P = 0.072$) of trampling intensity on total forb cover but not on grass cover. Lightly trampled plots had higher forb cover than heavily trampled and mod-

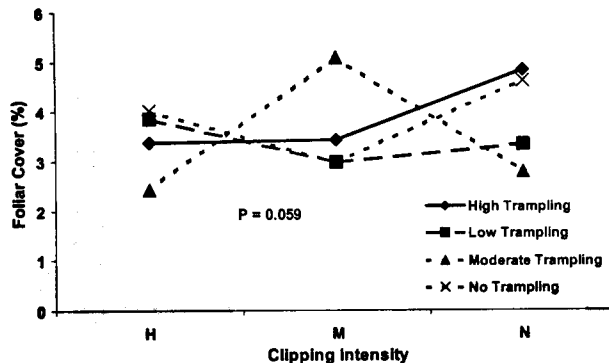


Fig. 4. Mean foliar cover (%) of grasses for different intensities of clipping X trampling treatment combinations in mixed-conifer enclosures (Spring 2000) - Bandelier National Monument, New Mexico. Clipping was applied at 0 (none), 40-60 (moderate), or 100% (heavy) standing crop removal while trampling was applied at 0 (none), 5 (light), 25 (moderate), or 100 (heavy) footfalls/unit area.

Table 1. Adjusted¹ mean density (number of plants/m² ± SE) by habitat for different intensities² of simulated clipping and trampling treatment combinations in 2000 on Bandelier National Monument, New Mexico.

Trampling Intensity	MC HABITAT ³				PG HABITAT				PJ HABITAT ⁴			
	Clipping Intensity			Mean ⁵ Trampling	Clipping Intensity			Mean ⁵ Trampling	Clipping Intensity			Mean ⁵ Trampling
	H	M	N		H	M	N		H	M	N	
H	366 (±48.18)	296 (±48.12)	350 (±48.11)	337A	81 (±17.64)	77 (±17.17)	87 (±17.20)	82A	53 (±6.46)	37 (±6.22)	54 (±6.26)	48A
M	333 (±48.13)	316 (±48.24)	303 (±48.11)	324A	127 (±17.17)	81 (±17.26)	101 (±17.82)	103A	53 (±6.25)	47 (±6.33)	39 (±6.30)	46A
L	352 (±48.30)	303 (±48.18)	319 (±48.39)	317A	86 (±17.22)	74 (±17.28)	93 (±17.21)	84A	56 (±6.32)	41 (±6.35)	36 (±6.47)	45A
N	379 (±50.36)	347 (±48.35)	355 (±48.30)	360A	70 (±17.17)	60 (±17.41)	10 (±21.55)	47A	52 (±6.22)	47 (±6.24)	49 (±6.36)	49A
Mean ⁵ Clipping	357A	315A	331A		91A	73A	73A		54A	43B	44B	

¹ ANCOVA adjusted means account for pre-treatment (1999) densities.

² Clipping was applied at 100 (H), 40-60 (M), or 0 (N) percent standing crop removal while trampling was applied at 100 (H), 25 (M), 5 (L), or 0 (N) footfalls per unit area.

³ MC = mixed-conifer, PG = ponderosa grassland, PJ = piñon-juniper.

⁴ Attempts to normalize data were unsuccessful and results should be interpreted with caution.

⁵ Means (within treatment) with the same letter are not statistically different at $\alpha = 0.10$.

Table 2. Adjusted¹ mean foliar cover (percent/m² ± SE) by vegetative type for different intensities² of simulated clipping and trampling treatment combinations in 2000 in piñon-juniper (PJ) habitat on Bandelier National Monument, New Mexico.

Trampling Frequency	FORBS				GRASSES			
	Clipping Intensity			Mean ³ Trampling	Clipping Intensity			Mean ³ Trampling
	H	M	N		H	M	N	
H	1.0 (±0.83)	2.6 (±0.83)	2.1 (±0.81)	1.9A (±0.48)	7.2 (±1.19)	8.4 (±1.20)	7.1 (±1.25)	7.6A (±0.69)
M	1.7 (±0.83)	1.5 (±0.81)	2.0 (±0.82)	1.7A (±0.47)	7.8 (±1.18)	7.8 (±1.19)	7.1 (±1.18)	7.6A (±0.68)
L	2.1 (±0.81)	4.2 (±0.81)	3.9 (±0.81)	3.4A (±0.47)	8.2 (±1.20)	7.7 (±1.20)	8.8 (±1.26)	8.2A (±0.74)
N	2.0 (±0.81)	2.7 (±0.81)	1.9 (±0.81)	2.2AB (±0.47)	6.7 (±1.26)	7.2 (±1.19)	9.8 (±1.18)	7.9A (±0.71)
Mean ³ Clipping	1.7A (±0.41)	2.7A (±0.40)	2.5A (±0.41)		7.5A (±0.60)	7.8A (±0.60)	8.2A (±0.59)	

¹ ANCOVA adjusted means account for pre-treatment (1999) foliar cover estimates.

² Clipping was applied at 100 (H), 40-60 (M), or 0 (N) percent standing crop removal while trampling was applied at 100 (H), 25 (M), 5 (L), or 0 (N) footfalls per unit area.

³ Means (within treatment) with the same letter are not statistically different at $\alpha = 0.10$.

Table 3. Mean litter cover (percent/m² ± SE) by habitat for different intensities¹ of simulated clipping and trampling treatment combinations in 2000 on Bandelier National Monument, New Mexico.

Trampling Intensity	MC HABITAT ²				PG HABITAT				PJ HABITAT ³			
	Clipping Intensity			Mean ⁴ Trampling	Clipping Intensity			Mean ⁴ Trampling	Clipping Intensity			Mean ⁴ Trampling
	H	M	N		H	M	N		H	M	N	
H	48.8 (±12.63)	66.0 (±15.87)	66.8 (±15.89)	60.5 A	12.1 (±5.80)	20.3 (±7.47)	18.8 (±1.51)	17.1 A	6.3 (±3.95)	11.1 (±8.50)	5.4 (±2.17)	7.6 A
M	74.8 (±10.61)	64.4 (±13.30)	64.6 (±15.02)	68.0 A	30.8 (±10.30)	22.3 (±3.36)	21.5 (±7.75)	24.8 AB	6.0 (±2.79)	3.4 (±1.05)	26.7 (±17.41)	12.0 A
L	54.4 (±14.72)	64.4 (±8.35)	67.6 (±15.56)	62.1 A	34.4 (±18.39)	31.2 (±10.23)	26.6 (±2.30)	30.7 A	4.0 (±0.52)	15.5 (±8.59)	31.4 (±18.42)	17.0 A
N	58.4 (±13.54)	57.4 (±13.12)	88.0 (±6.23)	67.9 A	11.3 (±3.21)	14.0 (±2.00)	29.8 (±14.13)	18.4 B	3.7 (±1.44)	5.3 (±2.25)	10.9 (±2.27)	6.6 A
Mean ⁴ Clipping	59.1 A	63.1 AB	71.8 A		22.1 A	22.0 A	24.2 A		5.0 A	8.8 AB	18.6 B	

¹ Clipping was applied at 100 (H), 40-60 (M), or 0 (N) percent standing crop removal while trampling was applied at 100 (H), 25 (M), 5 (L), or 0 (N) footfalls per unit area.

² MC = mixed-conifer, PG = ponderosa grassland, PJ = piñon-juniper.

³ Attempts to normalize data were unsuccessful and results should be interpreted with caution.

⁴ Means (within treatment) with the same letter are not statistically different at $\alpha = 0.10$.

erately trampled plots (Table 2).

Clipping had an effect ($F_{2,44} = 3.46, P = 0.04$) on litter cover in the PJ habitat; however, data were not normally distributed and results should be interpreted with caution. Mean separation revealed greater litter cover in non-clipped plots than in heavily clipped areas (Table 3).

Relative species composition changed (Table 4). Blue grama (*Bouteloua gracilis*) and deervetch (*Lotus wrightii*) increased across all treatment combinations in 2000, whereas mountain muhly and yellow ragweed (*Bahia dissecta*) decreased. However, this difference was relatively consistent regardless of clipping/trampling treatment. Snakeweed (*Gutierrezia sarrothrae*), however, tended to increase as clipping/trampling intensity increased. This may indicate a possible effect of treatment intensity. Mean basal area/plant was lower in 2000 than in 1999 ($F_{1,48} = 10.02, P = 0.003$) across all treatments probably due to abiotic (i.e., climate) factors.

Ponderosa-Grassland Habitat

Trampling affected plant density ($F_{3,21} = 4.14, P = 0.019$) regardless of clipping intensity. Non-trampled units had lower total density of plants than lightly, moderately, or heavily trampled units (Table 1). Trampling intensity also had an effect ($F_{3,21} = 4.10, P = 0.020$) on total density of forbs. Non-trampled units had fewer forbs than lightly, moderately, or heavily trampled units (Table 5).

Trampling had an effect ($F_{3,22} = 2.51, P = 0.085$) on total litter cover. Lightly trampled units had more litter cover than non-trampled and heavily trampled units but did not differ from moderately trampled plots (Table 3).

Species compositional shifts were evident with a few select species. Western wheatgrass (*Agropyron smithii*) proliferated in response to moderate levels of tram-

pling as it shifted from 13.1% of total community in 1999 to becoming the dominant species at 29.6% in spring of 2000. Trailing fleabane (*Erigeron flagellaris*) increased with increasing trampling intensity and moderate levels of clipping. Heavy clipping and trampling had a deleterious effect on Arizona three-awn (*Aristida arizonica*) as it decreased in relative composition (-2.28%) compared to an increase (+7.96%) when no treatments were applied. Goosefoot (*Chenopodium* spp.) disappeared from all treatments. Golden aster (*Chrysopsis villosa*) decreased (-3.23%) in relative composition at the highest levels of clipping/trampling. However, it appeared to be more sensitive to trampling as decreases in its relative composition increased at greater trampling intensities (Table 4). Mean basal area/plant was lower in 2000 than in 1999 ($F_{1,24} = 3.65, P = 0.068$) as a probable result of abiotic factors, but no changes in mean basal area/plant or species richness were detected for clipping, trampling, or their interaction.

Mixed-Conifer Habitat

Clipping X trampling treatment combinations had an effect ($F_{6,22} = 2.34, P = 0.048$) on total foliar cover of grasses (Fig. 4). There was an increase in grass cover at moderate intensities of trampling coupled with moderate intensities of clipping. For all other clipping intensities, grass cover decreased at moderate levels of trampling. In addition, clipping had an effect ($F_{2,44} = 2.52, P = 0.092$) on litter cover. Non-clipped plots had more litter than heavily clipped plots (Table 3).

Trampling had an effect ($F_{3,43} = 2.25, P = 0.096$) on the total number of species. Lightly trampled plots had more species ($\bar{X} = 10$) than heavily trampled ($\bar{X} = 8, P = 0.032$) areas, but not than moderately trampled ($\bar{X} = 9, P = 0.132$) or non-trampled ($\bar{X} = 10, P = 0.845$) sites. Mean basal area/

Table 4. Relative composition (%) of common species in 1999 vs. 2000 by habitat for different intensities¹ of clipping and trampling treatment combinations on Bandelier National Monument, New Mexico.

	Clipping Intensity						Trampling Intensity							
	Heavy		Moderate		None		Heavy		Moderate		Light		None	
	1999	2000	1999	2000	1999	2000	1999	2000	1999	2000	1999	2000	1999	2000
Mixed-Conifer Habitat														
<i>Poa</i> ssp.	183	220	194	206	146	136	224	203	134	186	247	189	32	175
<i>Bromus</i> ssp.	8.3	5.7	6.8	7.6	4.5	4.8	8.2	7.3	5.0	6.2	5.7	6.2	8.5	4.4
<i>Carex</i> ssp.	5.2	9.0	2.7	9.4	10.0	13.9	3.7	7.4	4.9	17.9	4.4	6.5	13.0	11.2
<i>Trifolium repens</i>	8.1	5.6	7.2	4.7	4.5	7.2	9.2	14.0	6.9	1.6	5.0	2.0	6.6	5.2
<i>Taraxacum officinale</i>	6.2	6.2	4.3	6.2	4.1	5.5	4.2	3.9	4.5	5.7	6.3	6.1	5.8	7.4
<i>Fragaria americana</i>	4.8	6.5	6.8	6.0	4.4	8.3	3.9	5.8	6.5	6.6	6.3	6.7	5.7	8.5
<i>Antennaria</i> ssp.	4.4	8.6	2.7	3.9	4.3	5.3	5.5	6.8	5.2	5.2	2.3	4.5	3.5	7.6
<i>Achillea lanulosa</i>	4.1	5.2	6.4	6.0	6.0	5.6	4.0	5.0	10.0	7.3	4.5	5.8	4.9	4.4
<i>Erigeron</i> ssp.	3.9	8.8	4.2	4.1	4.3	4.8	3.3	4.8	2.7	3.0	9.2	13.0	2.6	3.8
<i>Galium boreale</i>	2.4	2.3	2.4	4.2	2.0	2.7	1.0	1.3	2.1	3.5	4.3	4.5	2.3	2.9
Ponderosa-Grassland Habitat														
<i>Agropyron smithii</i>	206	309	218	241	315	316	163	170	13.1	29.6	40.5	40.3	27.0	28.9
<i>Muhlenbergia montana</i>	206	19.1	16.8	16.9	11.8	13.2	31.7	29.9	18.7	11.9	17.6	18.5	3.3	6.7
<i>Bouteloua gracilis</i>	6.6	5.7	3.8	4.4	1.4	3.1	2.7	2.6	1.7	1.7	0.7	1.8	7.9	12.2
<i>Schizachrium scoparium</i>	2.1	2.5	2.3	2.6	1.7	2.8	1.7	2.0	2.7	2.0	1.6	3.3	2.1	3.3
<i>Aristida arizonica</i>	3.8	3.8	5.1	5.9	3.1	5.4	2.0	2.9	5.4	5.6	2.0	3.3	5.4	7.9
<i>Chrysopsis villosa</i>	10.3	6.5	4.9	4.5	6.8	4.9	4.8	2.3	9.4	5.1	6.8	5.2	7.7	8.8
<i>Bahia dissecta</i>	8.0	4.5	14.5	8.1	5.5	5.4	8.3	6.8	7.2	3.3	10.1	9.2	10.0	4.8
<i>Erigeron flagellaris</i>	7.4	11.1	3.4	13.5	3.0	4.5	3.6	17.3	5.0	9.4	4.1	5.0	4.9	7.0
<i>Artemesia</i> ssp.	3.3	2.6	3.4	4.5	7.4	17.0	4.1	8.2	11.6	16.6	1.1	1.8	3.1	3.6
<i>Lotus wrightii</i>	2.5	4.4	3.2	4.3	3.2	3.4	1.9	2.8	5.2	4.9	2.3	3.9	2.6	4.4
<i>Chenopodium</i> ssp.	—	—	5.3	0.0	13.3	0.0	5.6	0.0	2.4	0.0	1.1	0.0	14.0	0.0

Table 4, continued

Piñon-Juniper Habitat	26.5	37.0	29.6	40.1	36.3	43.7	32.4	48.9	34.4	46.3	25.7	35.6	35.9	45.0
<i>Bouteloua gracilis</i>	15.6	11.	17.7	9.7	19.0	15.4	17.6	16.4	17.5	14.4	13.4	3.1	18.3	12.6
<i>Muhlenbergia montana</i>	4.9	5.0	2.5	4.6	3.9	3.4	5.4	4.6	3.8	3.3	3.0	3.0	6.3	6.4
<i>Aristida purpurea</i>	0.6	1.0	0.7	1.6	0.6	1.5	—	—	2.0	2.7	—	—	0.4	1.7
<i>Schizachrium scoparium</i>	21.4	21.7	18.1	20.5	12.5	14.9	11.5	14.5	15.2	16.2	22.6	25.0	16.3	16.9
<i>Lotus wrightii</i>	6.0	2.5	3.9	1.3	3.0	1.6	2.5	0.0	3.6	0.9	4.6	1.6	1.6	0.5
<i>Bahia dissecta</i>	4.3	1.8	2.6	1.9	2.3	2.1	—	—	4.5	1.8	2.5	2.0	2.0	1.9
<i>Gutierrezia sarothrae</i>														

¹ Clipping was applied at 100 (Heavy), 40-60 (Moderate), or 0 (None) percent standing crop removal while trampling was applied at 100 (Heavy), 25 (Moderate), 5 (Light), or 0 (None) footfalls per unit area.

plant was significantly less in 2000 than in 1999 ($F_{1,48} = 27.06, P < 0.001$). No other effects for clipping, trampling, or their interaction were detected for any other variable.

Shifts in species composition were pronounced (Table 4). Wild strawberry (*Fragaria americana*) decreased in relative composition at intermediate levels of clipping and trampling, but increased at the extremes. White clover (*Trifolium repens*) increased (+4.8%) at the highest trampling intensity, but decreased at all other levels. In addition, white clover increased 2.7% in non-clipped units, but decreased about 2.5% when moderate or heavy clipping was applied. The relative contribution of bluegrasses (*Poa* spp.) increased with increasing clipping intensity (+1.0%, 1.2%, and 3.7% for none, moderate, and heavy clipping, respectively). Moderate intensities of clipping and trampling increased the relative contribution of sedges (*Carex* spp.). Pussytoes (*Antennaria* spp.) increased with increasing clipping intensity (+1.0%, +1.2%, and +4.2% for none, moderate, and heavy clipping, respectively). Heavy intensities of clipping increased the relative contribution of fleabanes (*Erigeron* spp.) (+4.9%) and Western yarrow (*Achillea lanulosa*) (+1.1%). However, when combined with the heaviest intensity of trampling, Western yarrow increased 0.8% in relative composition compared to a 4.7% decrease when no clipping or trampling was applied.

DISCUSSION

During this study, BAND experienced two unseasonably warm years. Plant communities are influenced as much, if not more, by abiotic variables (e.g., inter-annual differences in growing season precipitation) than by ungulate populations (Peterson et al. 1997). Winkel and Roundy (1991) found seedling emergence in response to cattle trampling differed among years and treatments relative to precipitation patterns and periods of available water. Olson et al. (1985) indicated that

Table 5. Adjusted¹ mean density (number of plants/m² ± SE) by vegetative type for different intensities² of simulated clipping and trampling treatment combinations in 2000 in ponderosa-grassland (PG) habitat on Bandelier National Monument, New Mexico.

Trampling Intensity	FORBS ³				GRASSES			
	Clipping Intensity			Mean ⁴ Trampling	Clipping Intensity			Mean ⁴ Trampling
	H	M	N		H	M	N	
H	6 (±0.79)	6 (±0.72)	5 (±0.41)	6 A (±0.41)	39 (±14.48)	35 (±15.06)	54 (±14.52)	43 A (±8.36)
M	5 (±0.70)	5 (±0.70)	6 (±0.70)	5 A (±0.40)	83 (±14.45)	49 (±14.45)	42 (±15.76)	58 A (±8.62)
L	5 (±0.71)	5 (±0.73)	5 (±0.70)	5 A (±0.42)	48 (±14.50)	41 (±14.52)	58 (±14.45)	49 A (±8.41)
N	4 (±0.73)	3 (±0.74)	4 (±0.71)	4 B (±0.45)	43 (±14.47)	51 (±14.46)	30 (±15.35)	42 A (±8.51)
Mean ⁴ Clipping	5 A (±0.35)	5 A (±0.35)	5 A (±0.35)		53 A (±7.23)	44 A (±7.24)	46 A (±7.23)	

¹ ANCOVA adjusted means account for pre-treatment (1999) foliar cover estimates.

² Clipping was applied at 100 (H), 40-60 (M), or 0 (N) percent standing crop removal while trampling was applied at 100 (H), 25 (M), 5 (L), or 0 (N) footfalls per unit area.

³ Density data for forbs were square root transformed to meet assumptions of normality.

⁴ Means (within treatment) with the same letter are not statistically different at $\alpha = 0.10$.

each species reacts to precipitation regimes and grazing pressure in a unique manner.

Given the migrational behavior of elk, elevational partitioning occurs in different seasons resulting in heavier use of certain habitats during some parts of the year. Impacts caused by clipping and/or trampling may be confounded when looking at individual plant species or differing precipitation regimes (Olson et al. 1985; Cole 1995a, b, 1998) all of which vary from one elevational zone to another. This may be somewhat illustrated by the inconsistent, but significant habitat X trampling interaction we detected for total foliar cover. Moderately trampled units in ponderosa habitats had 2.5 times more foliar cover than in PJ, and nearly 4 times more than in MC sites. However, within habitat analysis in PG did not reveal any trampling effects on foliar cover whereas a significant effect was detected in PJ.

Plant densities were higher in heavily clipped plots in PJ habitat versus moderately or non-clipped experimental units. It is possible that bunchgrasses in PJ sites responded to heavy clipping pressure coupled with above average seasonal temperatures and lower moisture with a breakup of the original plants, which were then counted as more individual plants the following year. Trampling applied to those plots exacerbated this effect by pulverizing the dead or dying connective portions of bunchgrasses. However, the dominant species in this habitat type was blue grama, which is deemed to be tolerant of grazing and trampling (USDA Forest Service, Fire Effects Information System, <http://www.fs.fed.us/database/feis>, March 12, 1998).

Intensity of clipping did not have any detectable effect on overall plant densities in PG habitat; however, clipping appeared to interact with trampling intensity in MC sites. Moderately grazed and trampled units tended to have relatively higher grass cover than any other treatment combination

in these sites. A clear explanation for this is not available, although other studies have advocated use of grazing or trampling to stimulate forage production (Savory and Parsons 1980, McNaughton et al. 1983). Though not supported by results in other habitats, it is possible that moderate intensities of clipping and trampling complement each other providing optimum growing conditions for grasses in MC habitats.

One result that appeared to be consistent regardless of habitat was the effect of clipping intensity on total litter cover. Less litter cover was found in heavily clipped plots in PJ and MC exclosures. A negative correlation of grazing intensity to litter cover has been documented elsewhere (Biondini et al. 1998). Litter plays a crucial role in ecosystems as a source of organic material and reducing soil erosion (Biondini et al. 1998).

Measures of basal area did not change with this first year's treatments and species richness was only affected by treatments in MC sites where heavy intensities of trampling resulted in fewer species. Such inconsistencies or lack of response can be explained in two ways. First, only a single year has elapsed between initial treatment applications and the resultant data collection reported here. Much longer time periods – periods in the range of 20 years – may be needed to detect some vegetative responses to changes in grazing pressure (Chong 1992) especially in ecosystems that have developed with a history of grazing pressure. Changes in basal cover for individual plant species may be highly susceptible to precipitation (Olson et al. 1985) indicating that dominant species and their response to precipitation fluctuation need to be identified over the long-term prior to evaluating grazing/trampling effects. Secondly, all vegetative parameters measured had high intrinsic variability.

At lower elevations blue grama in-

creased with a subsequent decrease in mountain muhly. Blue grama is known to be tolerant of grazing (Santos and Trlica 1978, Bock and Bock 1986) and may even increase in overgrazed range (USDA Forest Service, Fire Effects Information System, <http://www.fs.fed.us/database/feis>, March 12, 1998). In contrast, mountain muhly is considered intolerant to grazing (Arnold 1950). In an Arizona study using long-term exclosures, Arnold (1950) indicated that mountain muhly showed the greatest increase in ungrazed quadrats, occurred in "patches" when moderately grazed, and disappeared when overgrazed. Similarly, in Colorado cover increased as grazing decreased (Johnson 1956) comprising 20% of the composition in ponderosa habitat on heavily grazed areas compared to 45% on those not grazed. Results of this study support these patterns.

Seasonal progression of environmental variables and phenological development of individual plants may confound effects of defoliation intensity (Briske and Richards 1995). Climate may confound interpretation since blue grama is more commonly known to be drought-tolerant (U.S. Forest Service 1937; Menke and Trlica 1981; USDA Forest Service, Fire Effects Information System, <http://www.fs.fed.us/database/feis>, March 12, 1998) – a condition which appears to be prevalent the last couple of years in this region of the Jemez Mountains. Boryslawski and Bentley (1985) reported an interaction between temperature regime and clipping treatment with blue grama being less sensitive to clipping at higher temperatures than western wheatgrass.

At mid-elevational ponderosa grassland sites, western wheatgrass proliferated in response to moderate levels of trampling. Wheatgrass is drought- and grazing-tolerant and is good winter forage for elk and mule deer (*Odocoileus hemionus*) (U.S.

Forest Service 1937), but it is known to be less tolerant to clipping at higher temperatures than blue grama (Boryslawski and Bentley 1985). To date our results support this observation.

Other notable shifts in species composition in PG included the disappearance of goosefoot species and an increase in trailing fleabane. Trailing fleabane is relatively poor forage because of its ground-level growth form and generally increases on grazed lands (U.S. Forest Service 1937). The disappearance of goosefoot species in our sites cannot be explained because of a lack of information on responses to grazing and trampling in the literature. However, treatments were applied at the earliest part of the growing season when these plants were seedlings and were probably unable to tolerate such extreme conditions.

Arizona three-awn decreased in relative composition when heavy clipping or trampling was applied, but increased on non-treated units. Little information exists in the literature regarding response to grazing pressure, but it is generally thought to have poor forage value because of its prominent awns (U.S. Forest Service 1937). In mixed-conifer regions, noticeable shifts in relative composition occurred with white-clover, bluegrasses, sedges, and pussytoes. White clover is considered excellent forage for ungulates (USDA Forest Service, Fire Effects Information System, <http://www.fs.fed.us/database/feis>, March 12, 1998) and withstands trampling well (U.S. Forest Service 1937), but it is not tolerant of drought conditions (Gibson and Cope 1985). Our results support this observation with the greatest relative increases in white clover occurring at the heaviest intensity of trampling. Though not evident with this study, plants can adapt to severe defoliation by developing smaller leaves and more stolons (Ryle et al. 1989) and it has been reported that this plant may grow stronger

and bulkier (i.e., become more robust) when grazed (U.S. Forest Service 1937, Hay et al. 1989, Chapman et al. 1992). In addition, white clover is a species with a high degree of phenotypic plasticity that can result in large fluctuations in size of individual plants (Hay et al. 1989).

Individual species of *Carex*, *Poa*, and *Antennaria* respond to grazing pressures and climate differently (U.S. Forest Service 1937) making it difficult to interpret our results which are based on generic classifications. In general, *Poa* spp. are known to be good to excellent forage and resistant to heavy trampling, grazing, and drought conditions (U.S. Forest Service 1937, Stubbendieck et al. 1985) because growing points are below ground throughout the growing season for most species (Ehrenreich and Aikman 1963). Results from this study support these observations as *Poa* spp. increased with increasing clipping intensity. Similarly, *Carex* spp. did not appear to be negatively impacted by grazing and trampling treatment combinations. Intermediate intensities of clipping and trampling increased the relative contribution of *Carex* in our study and it did not appear to benefit when protected from grazers. Likewise, *Antennaria* spp. increased with clipping intensity. One species, *A. parvifolia*, has been shown to decrease slightly under light to moderate grazing, but increase in heavily grazed areas (Smith 1967). In ponderosa communities, it has also been shown to survive heavy trampling (Smith 1967).

Trampling, in general, more consistently affected variables. In PJ communities, moderately trampled plots had less total foliar cover than lightly trampled units. Further inspection indicated that lightly trampled treatments had significantly higher forb cover in this community. In contrast, moderately trampled units had a higher density of plants than non-trampled areas in PG, but densities were not different from lightly or

heavily trampled sites. Finally, MC sites had more species in lightly trampled locations compared to heavily treated areas, but not when compared to moderately or non-trampled quadrats. In total, these observations suggest that there may be an intermediate threshold at which trampling may stimulate plant productivity, especially in terms of forb response.

Similar responses to trampling have been reported in the literature. Cole and Spildie (1998) concluded forb-dominated sites were highly vulnerable to trampling effects, but recovered rapidly. The ability of a vegetation type to tolerate recurrent trampling disturbance may be more a function to recover from damage than its ability to resist being damaged (Cole 1995a, b). Cole (1995a, b) further stated that certain vegetation types might exhibit thresholds of vulnerability in response to trampling that, when exceeded, may result in even greater damage to the plant.

There are 3 explanations for the variable results we found in this study. First, there may be a possibility that heavy winter and variable spring grazing, with associated trampling, may not cause extensive plant mortality or progressive changes in basal area (Houston 1982), especially during dormant phases of plant life cycles. Secondly, much longer time periods (periods in the range of 20 years) may be needed to detect vegetative responses to changes in grazing pressure (Chong 1992), especially in ecosystems that have developed with a history of grazing pressure. Finally, the amount of inherent variability present in the vegetative communities of BAND may have precluded detection of changes.

ACKNOWLEDGEMENTS

We would like to thank Cindy Caplen, Erika Hersch, Salinda Daley, Doug Krantz, Christine Evans, and Eric Wolf for their assistance in the field as well as Bandelier

National Monument for their financial and research assistance. This is Texas Tech University, College of Agricultural Sciences and Natural Resources technical publication T-9-892 and Los Alamos National Research Laboratory publication LA-UR-01-1955.

REFERENCES

- ABDEL-MAGID, A. H., M. J. TRLICA, and R. H. HART. 1987. Soil and vegetation responses to simulated trampling. *Journal of Range Management* 40:303-306.
- ALLEN, C. D. 1996. Elk response to the La Mesa Fire and current status in the Jemez Mountains. Pages 179-195 in C. D. Allen, editor. *Fire effects in Southwestern forests: Proceedings of the second La Mesa Fire symposium*. RM-GTR-286. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- ARNOLD, J. F. 1950. Changes in ponderosa pine bunchgrass ranges in northern Arizona resulting from pine regeneration and grazing. *Journal of Forestry* 48: 118-126.
- BASTRENTA, B., J. LEBRETON, and J. D. THOMPSON. 1995. Predicting demographic change in response to herbivory: a model of the effects of grazing and annual variation on the population dynamics of *Anthyllis vulneraria*. *Journal of Applied Ecology* 83:603-611.
- BIONDINI, M. E., B. D. PATTON, and P. E. NYREN. 1998. Grazing intensity and ecosystem processes in a northern mixed-grass prairie, USA. *Ecological Applications* 8:469-479.
- BOCK, J. H., and C. E. BOCK. 1986. Habitat relationships of some native perennial grasses in southeastern Arizona. *Desert Plants* 8: 3-14.
- BORYSLAWSKI, Z., and B. L. BENTLEY. 1985. The effect of nitrogen and clipping on interference between C₃ and C₄ grasses. *Journal of Ecology* 73:113-121.
- BRISKE, D. D., and J. H. RICHARDS. 1995. Plant responses to defoliation: a physiological, morphological and demographic evaluation. Pages 635-710 in D. J. Bedunah, editor. *Wildland plants: physiological ecology and developmental morphology*. Society for Range Management, Denver, Colorado, USA.
- BROWN, D. E. 1982, editor. *Biotic communities of the American Southwest-United States, and Mexico*. *Desert Plants* 4(1-4):1-342.
- CHAPMAN, D. F., M. J. ROBSON, and R. W. SNAYDON. 1992. Interactions between defoliation and the nitrogen nutrition of white clover (*Trifolium repens* L.): effects on carbon utilisation in clonal plants. *Plant and Soil* 139:157-165.
- CHONG, G. W. 1992. Seventeen years of grazer exclusion on 3 sites in piñon-juniper woodland at Bandelier National Monument, New Mexico. Unpublished Report, Bandelier National Monument, Los Alamos, New Mexico, USA.
- COLE, D. N. 1995a. Experimental trampling of vegetation. I. Relationship between trampling intensity and vegetation response. *Journal of Applied Ecology* 32:203-214.
- _____. 1995b. Experimental trampling of vegetation. II. Predictors of resistance and resilience. *Journal of Applied Ecology* 32:215-224.
- _____. 1998. Disturbance and recovery of trampled montane grassland and forests in Montana. USDA Forest Service Intermountain Research Station, Ogden, Utah, USA.
- _____, and D. R. SPILDIE. 1998. Hiker, horse and llama trampling effects on native vegetation in Montana, USA. *Journal of Environmental Management* 53:61-71.
- EHRENREICH, J. H., and J. M. AIKMAN. 1963. An ecological study of the effect of

- certain management practices on native prairie in Iowa. *Ecological Monographs* 33: 113-130.
- FETTIG, S., editor. 1997. Environmental assessment of proposed evaluation of ungulate impacts to park resources: a research project using exclosures. Unpublished environmental assessment on file at Bandelier National Monument. USDA National Park Service, Bandelier National Monument, Los Alamos, New Mexico, USA.
- FOXX, T. S. 1984. La Mesa Fire Symposium. Pages 1-10 in Foxx, T. S., editor. La Mesa Fire Symposium. LA-9326-NERP. Los Alamos National Laboratory, Los Alamos, New Mexico, USA.
- GIBSON, P. B., and W. A. COPE. 1985. White clover. Pages 471-490 in N.L. Taylor, editor. Clover science and technology. American Society of Agronomy, Crop Science Society of America, Madison, Wisconsin, USA.
- GILLEN, R. L., F. T. MCCOLLUM, and J. E. BRUMMER. 1990. Tiller defoliation patterns under short duration grazing in tallgrass prairie. *Journal of Range Management* 43:95-99.
- HAY, M. J. M., J. L. BROCK, and V. J. THOMAS. 1989. Density of *Trifolium repens* plants in mixed swards under intensive grazing by sheep. *Journal of Agricultural Science* 113:81-86.
- HOUSTON, D. B. 1982. The Northern Yellowstone Elk. MacMillan Publishing, New York, New York, USA.
- JOHNSON, W. M. 1956. The effect of grazing intensity on plant composition, vigor, and growth of pine-bunchgrass ranges in central Colorado. *Ecology* 37:790-798.
- MCNAUGHTON, S. J., L. L. WALLACE, and M. B. COUGHENOUR. 1983. Plant adaptation in an ecosystem context: effects of defoliation, nitrogen, and water on growth of an African sedge. *Ecology* 64:307-318.
- MENKE, J. W., and M. J. TRLICA. 1981. Carbohydrate reserve, phenology, and growth cycles of nine Colorado range species. *Journal of Range Management* 34:269-277.
- MOTAZEDIAN, I. J., and S. H. SHARROW. 1990. Defoliation frequency and intensity effects on pasture forage quality. *Journal of Range Management* 43:198-201.
- OESTERHELD, M. 1992. Effect of defoliation intensity on aboveground and belowground relative growth rates. *Oecologia* 92:313-316.
- OLSON, K. C., R. S. WHITE, and B. W. SINDELAR. 1985. Response of vegetation of the northern Great Plains to precipitation amount and grazing intensity. *Journal of Range Management* 38:357-361.
- PETERSON, J., J. FAHNESTOCK, and J. K. DETLING. 1997. Ungulate/vegetation interactions at the Pryor Mountain Wild Horse Range. Bureau of Land Management Report, Cooperative Agreement Number 1268-1-9002. Department of Biology, Colorado State University, Fort Collins, Colorado, USA.
- RUPP, S. P., M. C. WALLACE, D. B. WESTER, S. FETTIG, and R. B. MITCHELL 2001. Effects of simulated elk grazing and trampling (II): Frequency. *Alces* 37:147-161.
- RYLE, G. J. A., C. E. POWELL, M. K. TIMBRELL, and J. P. JACKSON. 1989. Carbon and nitrogen yield, and N₂ fixation in white clover plants receiving simulated continuous defoliation in controlled environments. *Annals of Botany* 63:675-686.
- SANTOS, G. L., and M. J. TRLICA. 1978. Clipping effects on production and carbohydrate reserves of blue grama and western wheatgrass. Pages 384-386 in D. N. Hyder, editor. Proceedings of the

- 1st International Rangeland Congress, Denver, Colorado, USA. August 14-18, 1978.
- SAVORY, A., and S. D. PARSONS. 1980. The Savory grazing method. *Rangelands* 2:234-237.
- SMITH, D. R. 1967. Effects of cattle grazing on a ponderosa pine-bunchgrass range in Colorado. Technical Bulletin Number 1371. U.S. Department of Agriculture, Forest Service, Washington, D.C., USA.
- SOKAL, R. R., and F. J. ROHLF. 1995. *Biometry: the principles and practice of statistics in biological research*. Third edition. W. H. Freeman and Company, New York, New York, USA.
- STEEL, R. G. D., and J. H. TORRIE. 1980. The randomized complete block design: more than one observation per treatment per block. Pages 215-218 in *Principles and procedures of statistics: a biometrical approach*. Second edition. McGraw-Hill, New York, New York, USA.
- STUBBENDIECK, J., J. T. NICHOLS, and K. K. ROBERTS. 1985. Nebraska range and pasture grasses (including grass-like plants). E.C. 85-170. University of Nebraska, Department of Agriculture, Cooperative Extension Service, Lincoln, Nebraska, USA.
- TELFER, E. S., and J. P. KELSALL. 1984. Adaptation of some large North American mammals for survival in snow. *Ecology* 65:1828-1834.
- TOLLNER, E. W., G. V. CALVERT, and G. LANGDALE. 1990. Animal trampling effects on soil physical properties of two Southeastern U.S. utisols. *Agriculture Ecosystems and Environment* 33:75-87.
- U.S. FOREST SERVICE. 1937. *Range plant handbook*. U.S. Government Printing Office, Washington, D.C., USA.
- WARREN, S. D., T. L. THUROW, W. H. BLACKBURN, and N. E. GARZA. 1986. The influence of livestock trampling under intensive rotation grazing on soil hydrologic characteristics. *Journal of Range Management* 39:491-495.
- WEIGEL, J. R., C. M. BRITTON, and G. R. MCPHERSON. 1990. Trampling effects from short-duration grazing on tobosagrass range. *Journal of Range Management* 43:92-95.
- WILCOX, B. P., and D. D. BRESHEARS. 1994. Hydrology and ecology of piñon-juniper woodlands: conceptual framework. Pages 109-119 in D. W. Shaw, E. F. Aldon, and C. LoSapio, technical coordinators. 1995. Desired future conditions for pinon-juniper ecosystems. USDA Forest Service General Technical Report. RM-258. Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- WINKEL, V. K., and B. A. ROUNDY. 1991. Effects of cattle trampling and mechanical seedbed preparation on grass seedling emergence. *Journal of Range Management* 44:176-180.

CONTENTS

FOREWORD	i
JOURNAL NEWS	ii
IN MEMORIAM - Eric Wynn Cox	iii
SUMMER FOOD HABITS OF GRAY WOLVES IN THE BOREAL FOREST OF THE LAC JACQUES-CARTIER HIGHLANDS, QUÉBEC Jean-Pierre Tremblay, Hélène Jolicoeur, and Rolland Lemieux	1
ACCURACY IN MOOSE MANDIBLE SIZE VERSUS TOOTH WEAR ASSESSMENTS Brian McLaren and Richard Curran	13
MOOSE HUNTERS' PERCEPTIONS OF FOREST HARVESTING Réhaume Courtois, Jean-Pierre Ouellet, and Anne Bugnet	19
MOOSE HUSBANDRY AT THE COLUMBUS ZOO: THE NUTRITION ASPECT Lori Monska	35
MODELING MOOSE SIGHTABILITY IN SOUTH-CENTRAL BRITISH COLUMBIA James F. Quayle, A. Grant MacHutchon, and Douglas N. Jury	43
LOCAL COMMUNITY BASED MOOSE MANAGEMENT PLANS IN NORWAY Johan Danielsen	55
REDUCED COST OF REPRODUCTION IN MOOSE <i>ALCES ALCES</i> THROUGH HUMAN HARVEST	61
..... Göran Ericsson	
AN ASSESSMENT OF CATCH PER UNIT EFFORT TO ESTIMATE RATE OF CHANGE IN DEER AND MOOSE POPULATIONS	71
..... Ian W. Hatter	
CHANGES IN THE RELATIONSHIP BETWEEN PALMATE AND CERVINE ANTLERS IN MOOSE (<i>ALCES ALCES</i>) IN SOUTHEASTERN NORWAY	79
..... Jens H. Engan	
FOREST OWNERS AS MOOSE HUNTERS IN FINLAND Risto Heikkilä and Jukka Aarnio	89
THE ECONOMIC VALUE OF MOOSE IN NORWAY – A REVIEW Torstein Storaas, Hege Gundersen, Hege Henriksen, and Harry P. Andreassen	97
SEXUAL SEGREGATION IN MOOSE: EFFECTS OF HABITAT MANIPULATION R. Terry Bowyer, Becky M. Pierce, Lawrence K. Duffy, and Dale A. Haggstrom	109
PECULIARITIES OF DAILY MILK PRODUCTIVITY OF PECHORA TAIGA DOMESTICATED COW MOOSE AND THEIR INTERCONNECTION WITH REPRODUCTIVE FUNCTION Tatyana F. Vasilenko, Irine N. Sivoxa, Mikhail V. Kozhykhov, and Patrick R. Lemons II	123
EFFECTS OF SIMULATED ELK GRAZING AND TRAMPLING (I): INTENSITY Susan P. Rupp, Mark C. Wallace, David Wester, Stephen Fettig, and Robert Mitchell	129
EFFECTS OF SIMULATED ELK GRAZING AND TRAMPLING (II): FREQUENCY Susan P. Rupp, Mark C. Wallace, David Wester, Stephen Fettig, and Robert Mitchell	147
CO-MANAGEMENT - THE MANITOBA EXPERIENCE	163
..... Vince Crichton	
GENETIC VARIATION OF MICROSATELLITE DNA IN MOOSE IN QUÉBEC Matthew A. Cronin, John C. Patton, Réhaume Courtois, and Michel Crête	175
REPRODUCTIVE LIFE HISTORY AND FERTILITY OF MOOSE IN NORTH ASIA N.K. Zheleznov and L.M. Fox	189

(Continued on inside back cover)

MOOSE
Mark A. Keed
TEMPTS
nd Yosef Cohe
ED TO SEXUA

.....	227
.....	229
.....	230
.....	235
.....	236
.....	237

NY BUBENIK
EVIEW COM

ADDITIONAL COPIES

Available from: Lakehead University Bookstore, Thunder Bay, Ontario, Canada P7B 5E1
Alces 24-37 Price \$38.00 Canadian or \$30.00 U.S. each (including supplementary issues)
Alces 19-23 Price \$20.00 Canadian or \$15.00 U.S. each
Alces 11, 14, 16 \$20.00 Canadian or \$15.00 U.S. each
*formerly Proc. N. Am. Moose Conf. Workshop

Take cheques, money orders or purchase orders payable to Lakehead University Bookstore.
include 7% G.S.T., mailing and handling costs. *Prices are subject to change.*

ACKNOWLEDGEMENTS

worked long hours formatting and types

ES HOME